The Roles of Vertical and Horizontal Gradients of Abiotic Stress in Determining Regional Intertidal Diversity Patterns in the Northwest Straits

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Abstract

Large-scale patterns in species richness have been the focus of a substantial body of ecological research. However, the mechanisms underlying these patterns remain hotly debated. In this study, I investigated the underlying causes of a regional scale gradient in species richness in the Northwest Straits (the Strait of Juan de Fuca, the San Juan Islands, and Puget Sound). At the seaward terminus of this basin, intertidal habitats are buffered from overly harsh physical conditions by cool air temperatures, frequent cloud cover and fog, and heavy wave action. Intertidal habitats further east suffer increasing stress due to higher air temperatures, increased direct insolation, reduced wave action, and summer low tides that occur in the middle of the day. Correlated with this abiotic stress gradient is a steady decline in species richness from west to east.

I hypothesized that the regional scale richness patterns result from the interaction of the large-scale, climatically driven stress gradient along the east-west axis with the smaller-scale, tidally driven stress gradient along the vertical axis. Specifically, increasing physical stress on the horizontal axis should compress the vertical zones of species to the point where many cannot persist on the most stressful shores. The upper limits of sessile taxa are strongly, negatively correlated with increasing stress (measured as substrate temperature at +1.5 m) along the horizontal axis. Lower limits, however, are not as strongly influenced by the horizontal stress gradient, perhaps because the foraging range of strongly interacting consumers were also relatively independent of this stress gradient. As a result, the vertical range of most species investigated decreased from west to east.

If the interaction of upper and lower limits across multiple taxa does indeed influence species richness patterns as hypothesized above, then many typically western species should be able to survive in eastern habitats if their lower limits are experimentally extended downshore. Such a situation would arise if dominant consumers were prevented from setting lower limits. To investigate this prediction, I experimentally excluded a dominant predator (*Pisaster ochraceus*) near the upper limits of intertidal invertebrates at four sites along the regional scale gradient. *Pisaster* exclusions at the easternmost site resulted in dramatic changes in community structure, including the appearance of species that were otherwise extremely rare (e.g. *Semibalanus cariosus* and *Mytilus trossulus*). Because *Semibalanus* and *Mytilus* provide favorable habitat for smaller invertebrates, *Pisaster* exclusions resulted in a doubling of local species richness. The effects of *Pisaster* removal at other sites were minimal. Thus, the differential impact of the horizontal environmental gradient on the vertical distributions of consumers and prey can create dramatic differences in assemblage structure at the regional scale. A mechanistic understanding of ecological pattern over multiple spatial gradients, as demonstrated here, provides a framework on which to base predictions about biological responses to future perturbations such as climate change and species invasions.

(A more detailed description of this research is provided in: Harley, C.D.G. 2001. Environmental modification of biological interactions: a comparison across scales. Ph.D. dissertation, University of Washington.)